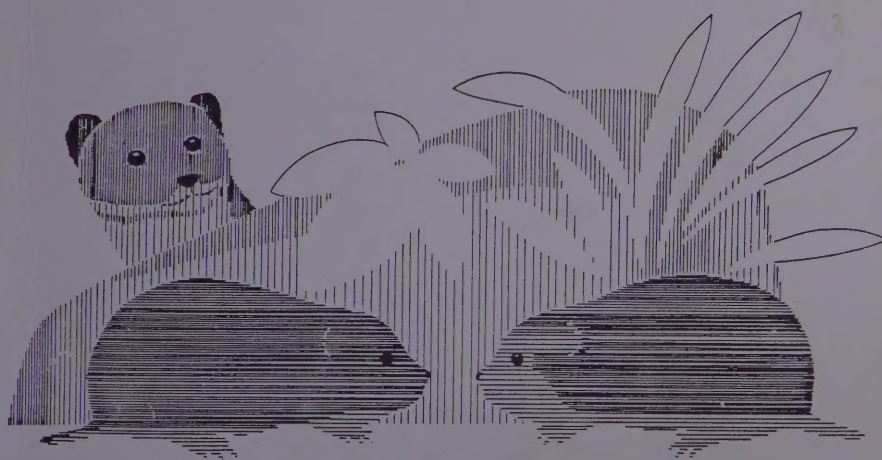


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Causes and geographic patterns of microtine cycles

Heikki Henttonen



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Causes and geographic patterns of microtine cycles

Heikki Henttonen

Department of Zoology and Kilpisjärvi Biological Station,
University of Helsinki, Finland

Academic dissertation

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Causes and geographic patterns of malaria cycles

Hanski Irmopuusti

Department of Zoology and Entomology, University of Helsinki, Finland
Institute of Zoology, University of Helsinki, Finland

Abstract. The causes and geographic patterns of malaria cycles are discussed. The main factors influencing the distribution of malaria are the climate, the distribution of the mosquito vector, and the distribution of the human host. The distribution of malaria is highly variable, and the causes of this variability are not fully understood. The geographic patterns of malaria cycles are also highly variable, and the causes of this variability are not fully understood.

*To Hilikka, Elina and Pentti –
a field biologist's family*

Causes and geographic patterns of microtine cycles

Heikki Henttonen

*Department of Zoology and Kilpisjärvi
Biological Station, University of Helsinki,
P. Rautatiekatu 13, SF-00100 Helsinki 10,
Finland*

This thesis is an abstract of the following publications, which are referred to in the text by their Roman numerals:

- I. Heikki Henttonen, Anthony D. McGuire and Lennart Hansson 1985. Comparisons of amplitudes and frequencies (spectral analyses) of density variations in long-term data sets of *Clethrionomys* species. — *Ann. Zool. Fennici* 22:221-227.
- II. Lennart Hansson and Heikki Henttonen 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. — *Oecologia* (Berlin) 67:394-402.
- III. Heikki Henttonen and Lennart Hansson 1986. Synchrony and asynchrony between sympatric rodent species with special reference to *Clethrionomys*. — *Holarct. Ecol.* (in press).
- IV. Kari Laine and Heikki Henttonen 1983. The role of plant production in microtine cycles in northern Fennoscandia. — *Oikos* 40:407-418.
- V. Heikki Henttonen, Tarja Oksanen, Aarre Jortikka and Voitto Haukisalmi 1986. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? — *Oikos* (in press).
- VI. Heikki Henttonen 1986. The impact of spacing behavior in microtine rodents on the dynamics of least weasels *Mustela nivalis* — a hypothesis. — *Oikos* (in press).

INTRODUCTION

Microtine cycles, once thought to be a feature characterizing the whole group of voles and lemmings (Elton 1942, Krebs and Myers 1974), have turned out to be something entirely different (I, II, III, Taitt and Krebs 1985). In this thesis, the first three publications quantitatively analyze geographic variation in density fluctuations of microtine rodents. I and my co-workers show that the patterns of microtine fluctuations are much more diversified and complicated than generally recognized. Perhaps the most essential message of these analyses is that there is no fixed pattern of *cycle*, and we cannot speak about *cyclic species*. No single mechanism alone can explain the variety of density fluctuations found in microtine rodents. In the jungle of ecological terms, *microtine cycle* may be the one most often incorrectly used.

Publications IV, V, and VI deal with the microtine dynamics in northern Fennoscandia (Finnish Lapland), where microtine fluctuations rather closely resemble what most ecologists understand by the term *cycle*. Several features strongly suggest that regulation important for cyclicity (steep population crash) is primarily due to extrinsic factors (IV, V, VI). Spacing behavior can prevent the unlimited growth of populations, but this should stabilize populations, not destabilize them in the extreme way regularly found in Lapland. Therefore, the papers IV, V, and VI try to differentiate between the resource- and predation-centered hypotheses.

J. B. S. Haldane (1927) once commented: "I have no doubt that in reality the future will be vastly more surprising than anything I can imagine. Now my own suspicion is that universe is not only queerer than we suppose, but queerer than we can suppose." The longer I have worked with microtine rodents and the more I have seen microtine populations with their various patterns of dynamics, the more I feel that Haldane had a strong intuition for these nice creatures.

MATERIAL AND METHODS

The analyses of geographic patterns (I, II, III) are based mainly on data in the literature, and to a minor extent on unpublished results of microtine studies in Fennoscandia. Time-series analyses (univariate spectral analyses) were performed for long-term data sets in *Clethrionomys* (I). However, when analyzing population dynamics of microtine rodents by time-series analyses, the paucity of long-term records is the major difficulty. Therefore, an index of cyclicity s (standard deviation of logarithmically — base ten — transformed density indices) was adopted in order to utilize the number of short-term studies available (II). The index of cyclicity s is greatest for data sets in which the 3–4 year frequency has the greatest contribution to the total spectral variance (I). Thus, even though s strictly taken measures only the relative variance (amplitude) of density fluctuations, it correlates well with the dominant wavelength of the spectral contribution to the time series (I). The coefficient of variation (CV), based on original untransformed density indices, gave the same results as s in geographic comparisons (II).

When analyzing geographic patterns of interspecific synchrony in microtine communities, we used a simple index describing the timing of the major decline in two species at a time (III). We preferred this robust index to more complicated covariance analyses because, from the point of view of population regulation — extrinsic or intrinsic — the timing of the deepest decline is the important feature. Multivariate analyses of the entire data sets would have included all the additional variation due to the differences in the timing of increases, and that due to the changes in peak densities of a species during successive cycles.

The botanical data from Kilpisjärvi has been gathered for various plant species from different habitats and altitudes (IV). Notice, however, that all the samples per a data point shown in IV (eg. Figs 2 and 3) are not

independent to the same degree (cf. Hurlbert 1984) because, e.g., for *Vaccinium myrtillus* there are three separate study sites, each including several small annual sample grids. Microtine data in relation to botanical indices are based on traditional linetrappings at Kilpisjärvi (IV).

Several kinds of data sets are combined in V (i) to show the patterns in a larger area in relation to the more intense studies at smaller sites (control of nondemonic intrusions), (ii) to test the impact of resource manipulations on microtine dynamics, and (iii) to analyze the role of small mustelids in the decline of a microtine cycle. The large-scale monitoring at Pallasjärvi has been performed by the Small Quadrat Method (Myllymäki et al. 1971) since 1971; in 1970 linetrappings were used (V). Livetrapping methods are described in detail in V. Twice yearly, snaptrappings accurately enough describe the general pattern as can be seen when they are compared with livetrapping data from the same habitat (V).

The information on weasel behavior in VI was derived from the literature because this kind of data is not available from Finnish Lapland. On the other hand, densities of *Clethrionomys* rodents on taiga habitats come from my own livetrapping studies (V, Henttonen 1980, unpubl.).

RESULTS

The main results are summarized below.

A. Geographic patterns

1. Time-series analyses (I) and those based on s (II) show clear regional patterns in the density variation of microtine rodents. In Fennoscandia there are distinct north — south gradients in density fluctuations of the two common species studied, cycles characterizing northern Fennoscandia and more seasonal variations characterizing southern Scandinavia and west-central Europe (II). In

the temperate European parts of the Soviet Union, the pattern seemed to be intermediate between the two regions mentioned above. These gradients are correlated with the duration and maximum thickness of snow cover. In North America such gradients were not found (II, Taitt and Krebs 1985), and snow cover did not explain the dynamics observed there (II).

2. There seems to be a basic difference in the microtine dynamics between northern Europe and northern parts of North America; cyclic *Clethrionomys* with a 4-5 year pattern are not known in North America, but they are characteristic of northern Fennoscandia (I, II). In North America, sympatric *Clethrionomys* and *Microtus* can show different patterns of density variation (one cyclic, another not); in northern Fennoscandia the whole microtine community characteristically shows a pronounced cyclicity (I, II, III, IV, V).

3. In Fennoscandia, temperate European parts of the Soviet Union and west-central Europe the degree of interspecific synchrony follows the pattern found in density variations: the more fluctuating (cyclic) the species are, the more simultaneous their deepest declines tend to be. Thus, pronounced cyclicity is correlated with a high degree of interspecific synchrony in the decline (III). This synchrony has been extended to include also shrew species (Hansson 1984, Henttonen 1985; see also Kaikusalo and Hanski 1985).

4. The strongly fluctuating (cyclic) populations are characterized by the continuation of the decline during the summer even if the major crash has occurred in the previous winter (II). This continuation of the decline is important in creating a time lag before the next increase. In noncyclic populations the densities usually increase during the summer (II).

B. Cycles in northern Fennoscandia

1. Cycles in northern Fennoscandia are characterized by a regular periodicity (I, Kaikusalo and Hanski 1985), great amplitu-

des (deep crashes) (II), and by a high degree of interspecific synchrony, especially in the decline (III). Therefore, hypotheses centering on resources and predation have been the prevailing ones when attempting to explain patterns in this region (V).

2. It seems evident that the importance of various extrinsic regulatory factors vary also in northern Fennoscandia. For example, overgrazing by the Norwegian lemming *Lemmus lemmus* especially in the alpine zone is well documented (Kalela 1971, Henttonen and Järvinen 1981, Oksanen and Oksanen 1981). On the other hand, predation might be a more probable reason for the synchronous crashes in forested habitats (III, V, VI).

3. Plant productivity as measured by variation in flowering intensity was correlated with microtine fluctuations at Kilpisjärvi (IV), but elsewhere in northern Fennoscandia contradicting results have been obtained (Oksanen and Oksanen 1981, Andersson and Jonasson 1986, Oksanen and Ericson 1986). It is also evident that variation in plant productivity alone cannot induce the deep crashes typical of northern Fennoscandia, i.e. predation is obviously heavily involved (IV, V, VI).

4. Distinct changes in the relative abundances of microtine species during successive cycles is typical in northern Fennoscandia (V, Henttonen et al. 1977). Changes in the abundances of small species could be due to interspecific competition (Henttonen and Hansson 1984), but this does not explain the changes in the competitively dominant species. It could be possible that long-term changes in plant production are involved (IV).

5. The latest, extended cycle in the northern Finnish taiga suggests that plant — microtine interactions may not be enough to trigger the steep crash of a typical four-year cycle (V). An extension of the peak phase during the latest cycle and the asynchrony among species during the slow decline occurred in the absence of least weasels *Muste-*

la nivalis. This provided a natural, although uncontrolled experiment. As a result it is suggested that small mustelids, least weasels in particular, may be important in starting the regular decline during the long nonbreeding season that occurs in the peak winter of microtines (V, VI). Weasels have usually been considered to only deepen and extend the crash phase (IV). The breeding performance of voles in the latest decline contradicts the common predictions derived from resource-centered hypotheses (V). However, I cannot totally exclude the possibility of more subtle forms of resource shortage affecting the survival of young instead of the breeding of adult voles.

6. Two kinds of resource manipulations were tested (V); these were (i) provision of supplementary food, and (ii) removal of voles during the snowless season for several years to prevent grazing, and then allowing access to this site by voles in the decline phase. Supplementary food increased densities showing that population density on a habitat depends on the food resources, but neither of the manipulations could change the general pattern of dynamics.

7. A hypothesis is put forward to explain the absence of least weasels during the latest cycle in northern taiga. I suggest that the lack of a numeric response by least weasels could have been due to the exceptionally low peak densities of the field vole *Microtus agrestis* (VI). According to my data, the spring and early summer densities of *Clethrionomys* species on taiga habitats do not exceed the threshold needed for successful breeding by female least weasels. I have no explanation for the exceptional population performance of *M. agrestis* during the latest cycle. However, the absence of least weasels could have resulted in the extended peak and in the slow and asynchronous decline. We could not prove that predation by stoats *Mustela erminea* alone was responsible for the gradual decline (V).

CONCLUSIONS

The wide array of fluctuation patterns in microtine rodents stresses the importance of comparative studies (I, II, and III), when monitoring population dynamics and when performing manipulative experiments. Differences in microtine dynamics within or between regions in relation to differences in animal communities and abiotic circumstances certainly create a background for relevant manipulative studies. Choosing a relevant experimental approach is greatly helped by an understanding of regional differences and hypothesized factors behind them, because the process of regulation is most probably not the same for cyclic and noncyclic microtine populations (cf. Chitty 1977). Too often everything is subsumed under a single *unifying* paradigm, and as a result interesting regional patterns are forgotten. I cannot help finding in microtine research some parallels with avian community ecology (Wiens 1983).

Most conclusions derived from manipulative studies to understand microtine cycles come from noncyclic populations. The criteria suggested by Watson and Moss (1970) to show that populations are regulated by socially-induced factors, will probably fit most microtine populations during their seasonal or cyclic peak density, be they cyclic or not. The common occurrence of social regulation or spacing behavior needs not to be related to cyclicity in any way. Even a genetic component in spacing behavior, and a consequent genetic time lag (Krebs 1979), cannot explain the steep crashes characteristic of strongly cyclic populations. For example, all natural *Clethrionomys* populations studied so far have the same social structure (Stenseth 1985), whether the population is cyclic, noncyclic or something intermediate. In *Microtus* the social systems are more diversified (Ostfeld 1985), but also in this genus there are cyclic and noncyclic populations within species (V, Taitt and Krebs 1985). It does not matter whether breeding males or

females are territorial, because in northern Fennoscandia sympatric species of both types undergo pronounced synchronous cycles. Therefore, I do not quite see the point in manipulating spacing behavior only to understand cyclicity. However, studies and manipulations of behavior produce interesting information as such. In addition, interspecific differences in spacing behavior may affect the microtine fluctuations in other ways as suggested in VI.

Spacing behavior should ultimately be determined by the environment. I do not consider other individuals of a species the most important environmental factor as regards cyclicity (cf. Chitty 1967, Krebs 1978). Evolutionary processes should not be restricted only to the genotypic-behavior hypothesis. Not to believe that spacing behavior drives cycles, is not anti-Darwinian thinking. For example, if predation by specialist mustelids causes the extreme crashes in northern Fennoscandia, as suggested in II, V, VI, and by Hansson (1984) and Henttonen (1985), then the most important selective pressure during the crash should be the ability to avoid predators. If the crash is due to resource shortage, adaptations to this should be the important selective force; for example polymorphism in relation to the changes of resource quality might develop. The deep crashes occurring regularly in northern Fennoscandia certainly are a strong selective force. On the other hand, it is self-evident that some noncyclic microtines on temperate grasslands undergo different selection pressures, produced e.g. by interaction between seasonal changes in food resources and spacing behavior.

The patterns that have emerged from the geographic comparisons (I, II, III) emphasize the view that predation is a more important factor, and the structure of local animal communities is more related to microtine fluctuations, than generally thought. The gradients found in Fennoscandia and their correlations with snow cover can be directly linked with different types of predation (II,

V, VI, Erlinge et al. 1983, Korpimäki 1986). However, ideas presented in this thesis about predation in northern Fennoscandia are still hypotheses, not definitely established facts. Consequently, they should be regarded as working hypotheses for future experimental studies. Even though the world is green, it does not mean that predation is everything everywhere, at least as far as our knowledge of microtine nutrition goes (cf. Batzli 1986).

The variety of regional patterns in microtine density fluctuations should force us to concentrate on the supposedly relevant differences in the biotic and abiotic factors between regions, and manipulate these factors. I give two conflicting examples. As natural *Clethrionomys* populations have a similar social structure, is it most productive to manipulate their social behavior to understand cyclicity? On the other hand, if specialist small mustelids are hypothesized to be the critical factor for cyclic *Clethrionomys* populations, similar weasel manipulations for cyclic and noncyclic *Clethrionomys* populations might result in interesting insights.

We must apparently accept a certain degree of minimalism (Slobodkin 1986) in the research of microtine cyclicity. One way to achieve this could be based on the results of comparative studies like the geographic analyses (I, II, III).

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References

- Andersson, M. and Jonasson, S. 1986. Rodent cycles in relation to food resources on an alpine heath. — *Oikos* 46: 93-106.
- Batzli, G. O. 1986. Nutritional ecology of the California vole: effects of food quality on reproduction. — *Ecology* 67: 406-412.
- Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. — *Proc. Ecol. Soc. Aust.* 2: 51-78.
- Chitty, D. 1977. Natural selection and the regulation of density in cyclic and non-cyclic populations. — In: Stonehouse, B. and Perrins, C. (eds), *Evolutionary Ecology*. The MacMillan Press Ltd., pp. 27-32.
- Elton, C. 1942. Voles, mice and lemmings: problems in population dynamics. Clarendon Press, Oxford.
- Erlinge, S., Göransson, G., Hansson, L., Högested, G., Liberg, O., Nilsson, I.N., Nilsson, T., Schantz, T. von, and Sylvén, M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. — *Oikos* 40: 36-52.
- Haldane, J. B. S. 1927. Possible Worlds and Other Papers. Chatto and Windus, London.
- Hansson, L. 1984. Predation as a factor causing extended low densities in microtine cycles. — *Oikos* 43: 255-256.
- Henttonen, H. 1980. Pohjois-Suomen pikkujyrsijöiden yhteisö rakenne ja lajien välinen kilpailu. (Community structure and interspecific competition among small rodents in northern Finland, in Finnish). — Unpubl. MS Thesis, Dept. Zool., Univ. Helsinki.
- Henttonen, H. 1985. Predation causing extended low densities in microtine dynamics: Further evidence from shrew dynamics. — *Oikos* 45: 156-157.
- Henttonen, H. and Hansson, L. 1984. Interspecific relations between small rodents in European boreal and subarctic environments. — *Acta Zool. Fennica* 172: 61-65.
- Henttonen, H. and Järvinen, A. 1981. Lemmings in 1978 at Kilpisjärvi: population characteristics of a small peak. — *Mem. Soc. Fauna Flora Fennica* 57: 25-30.
- Henttonen, H., Kaikusalo, A., Tast, J. and Viitala, J. 1977. Interspecific competition between small rodents in subarctic and boreal ecosystems. — *Oikos* 29: 581-590.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. — *Ecol. Monogr.* 54: 187-211.
- Kaikusalo, A. and Hanski, I. 1985. Population dynamics of *Sorex araneus* and *S. caecutiens* in Finnish Lapland. — *Acta Zool. Fennica* 173: 283-285.
- Kalela, O. 1971. Seasonal differences in the habitats of the Norwegian lemming, *Lemmus Lemmus* (L.), in 1959 and 1960 at Kilpisjärvi, Finnish Lapland. — *Ann. Acad. Sci. Fenn. (A IV)* 178: 1-22.
- Korpimäki, E. 1986. Predation causing synchronous decline phases in microtine and shrew populations in western Finland. — *Oikos* 46: 124-127.
- Krebs, C. J. 1978. A review of the Chitty Hypothesis of population regulation. — *Can. J. Zool.* 56: 2463-2480.
- Krebs, C. J. 1979. Dispersal, spacing behaviour, and genetics in relation to population fluctuations in the vole *Microtus townsendii*. — *Fortschr. Zool.* 25: 61-77.

- Krebs, C. J. and Myers, J. H. 1974. Population cycles in small mammals. — *Adv. Ecol. Res.* 8: 268-389.
- Myllymäki, A., Paasikallio, A., Pankakoski, E. and Kannervo, V. 1971. Removal experiments on small quadrats as a means of rapid assessment of the abundance of small mammals. — *Ann. Zool. Fennici* 8: 177-185.
- Oksanen, L. and Oksanen, T. 1981. Lemmings (*Lemmus lemmus*) and grey-sided voles (*Clethrionomys rufocanus*) in interaction with their resources and predators on Finnmarksvidda, northern Norway. — *Rep. Kevo Subarctic Res. Stat.* 17: 7-31.
- Oksanen, L. and Ericson, L. 1986. Dynamics of tundra and taiga populations of herbaceous plants in relation to the Tihomirov-Fretwell and Kalela-Tast hypotheses. — *Oikos* (in press).
- Ostfeld, R. S. 1985. Limiting resources and territoriality in microtine rodents. — *Am. Nat.* 126: 1-15.
- Slobodkin, L. B. 1986. The role of minimalism in art and science. — *Am. Nat.* 127: 257-265.
- Stenseth, N. C. 1985. Models of bank vole and wood mouse populations. — *Symp. Zool. Soc. London* 55: 339-376.
- Taitt, M. J. and Krebs, C. J. 1985. Population dynamics and cycles. — In: Tamarin, R. H. (ed.), *Biology of New world Microtus*. Spec. Publ. No. 8, Am. Soc. Mammal., pp. 567-620.
- Watson, A. and Moss, R. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. — In: Watson, A. (ed.), *Animal populations in relation to their food resources*. Blackwell Scient. Publ., Oxford, pp. 167-218.
- Wiens, J. A. 1983. Avian community ecology: an iconoclastic view. — In: Brush, A. H. and Clark, G. A., Jr. (eds), *Perspectives in ornithology*. Cambridge Univ. Press, pp. 355-403.

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